Housing of ringtailed lemur, *Lemur catta*, from an ethological perspective

Hållning av ringsvanslemur, lemur catta, ur ett etologiskt perspektiv

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Photo: Taina Thernström

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I denna serie publiceras olika typer av studentarbeten, bl.a. examensarbeten, vanligtvis omfattande 7,5-30 hp. Studentarbeten ingår som en obligatorisk del i olika program och syftar till att under handledning ge den studerande träning i att självständigt och på ett vetenskapligt sätt lösa en uppgift. Arbetenas innehåll, resultat och slutsatser bör således bedömas mot denna bakgrund.

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On the cover: Ringtailed lemur mother with infant at Ystad djurpark.

1. ABSTRACT

When housing animals at zoos many factors have to be taken in consideration regarding the visitors, the zoo and the animals. Ethology is an important element and the understanding of it is essential to animals' welfare and wellbeing. Compared to other primates little research has been done on lemurs. The aim of this literature study is to look further into the natural behaviour of the ringtailed lemur (*Lemur catta*) and how housing of the ringtailed lemur can be optimized from an ethological perspective. The ringtailed lemur is found on Madagascar and is a group-living primate where females are dominant over males. They live in different types of habitats with heavy fluctuations in rainfall and temperature. An optimal group size in captivity is 10-15 group members including no more than seven females. Appropriate exhibit enclosures should have three sides away from public view, multiple nesting boxes, stable and "moving" furnishing and hiding places. The lemurs should also have access to both indoor and outdoor enclosures all year round. Examples of environmental enrichments are different kinds of foraging tasks that are both time and energy consuming.

2. SAMMANFATTNING

Vid hållandet av djur i djurpark så är det många faktorer som måste tas i beaktande när det gäller besökarna, djurparken och djuren. Etologi är en viktig faktor och förståelsen för den är viktig för djurens välbefinnande och välmående. Jämfört med andra primater har det gjorts relativt lite forskning på lemurer. Syftet med denna litteraturstudie är att närmare granska ringsvanslemurens (*Lemur Catta*) naturliga beteende och hur hållandet av arten kan optimeras ur ett etologiskt perspektiv. Ringsvanslemuren härstammar från Madagaskar och är en dagaktiv och grupplevande primat där honorna är dominanta över hanarna. Lemurer lever i olika typer av habitat med stora variationer i nederbörd och temperatur. En optimal gruppstorlek består av ca 10 gruppmedlemmar med högst sju honor. Lämpliga visningshägn bör ha tre sidor fria från insyn, flera boholkar, fast och rörlig inredning och gömställen. Lemurerna bör även ha tillgång till både inomhus- och utomhushägnen hela året. Exempel på miljöberikningar är olika typer av födosöksuppgifter som är både tids- och energikrävande.

3. INTRODUCTION

The lemurs of Madagascar are one of the most endangered primates in the world because of habitat loss and degradation, hunting and exceptional endemism (Sauther et al., 2006). From the time when humans arrived at Madagascar approximately 2000 years ago the entire endemic mega fauna, including all species of giant lemurs, has gone extinct (Muldoon, 2010) and archaeological findings suggest that lemurs have been part of the native's diet since then (Garcia & Goodman, 2003).

Of all members of the family *Lemuridae* the ringtailed lemur is most abundant in zoos (Dishman et al., 2009). More than 300 zoos all over the world and several zoos in Sweden are currently housing them. Despite this there is still much research left to do to before we have completely mapped their behavioural ecology and subsequently are able to improve their welfare in zoos all over the world.

There has been a dramatic improvement of the housing of animals and the design of enclosures since the first zoos were established in the 19th century. Despite this, mainly stress but also stereotypic behaviour are common features in the lives of captive primates.

Generally, husbandry manuals are mainly focusing on the housing requirements of the animals without taking natural ethology or enrichments in consideration although behaviour is integrated in almost every aspect of the housing. Additionally, much of the research that has been conducted on lemurs has been done with the aim of understanding human evolution and thus important areas have been overlooked.

4. AIM

The aim of this literature study is to look further into the natural behaviour of the ringtailed lemur. The question I want to find an answer to is: ”How can housing of ring-tailed lemur, *Lemur catta*, be optimized from an ethological perspective?” Helpful to answer this question are the following sub questions: (1) how should appropriate enclosures for ringtailed lemurs be designed? and (2) what would be suitable environmental enrichments for ringtailed lemurs? and finally (3) what would be the optimal social structure for ringtailed lemurs in captivity?

This literature study addresses zoos and how they can house ringtailed lemurs while taking the natural ethology and behaviour of this species into consideration. Depending on the basic level of knowledge about this species in the zoos this literature study is more or less useful to them.

5. MATERIAL AND METHOD

This paper is a literature study and prior to and during this course I have been searching for and read scientific articles and books about ringtailed lemurs. Key words that I have used are for example "*Lemur catta*", "ethology", "behaviour" and "socioecology". Specific journals that I have searched for articles in are "Animal Behavior", "Hormones and behavior", "Journal of Human Evolution", "Applied Animal Behaviour Science", Behavioural Processes", "TRENDS in Genetics" and "Evolutionary Anthropology".

I have been in contact with the Lemur conservation foundation and I also visited two zoos that keep ringtailed lemurs to study and ask questions about ringtailed lemur husbandry. I visited Ystad djurpark in Ystad on the 12th of May and I visited Tropikariet in Helsingborg on the 14th of May. The aim of the visits was to get an insight in how ringtailed lemurs are housed practically and also to personally meet ringtailed lemurs. I asked the zoologists and the animal keepers questions about the husbandry of and the environmental enrichment for their ringtailed lemurs and also if they would like to change anything regarding the enclosures. I looked at the design and the position of the enclosures and their furnishing, enrichments and the group structures in these two zoos. Since the visits were done on my own account I will not further discuss the lemur husbandry of the two zoos in question.

6. RESULTS

6.1 Lemur biology

6.1.1 Taxonomy

The ring-tailed lemur, *Lemur catta*, belongs to the order *Primates*, the suborder *Stresirrhini* (Eaglen & Groves, 1988), the infraorder *Lemuriformes* (Yoder, 2007), the family *Lemuridae*, the genus *Lemur* and the species *Lemur catta* (Eaglen & Groves, 1988). Lemurs are prosimian primates (Kappeler, 1990) which mean that they are neither apes nor monkeys. Other names are Maki (Malagasy, which is the language spoken in Madagascar), lemur colianillado (Spanish), lémur catta (French) and ringsvanslemur (Swedish). The word *lemurēs* derive from Latin and means "spirits of the dead". Figure 1. shows the primate phylogeny and when divergence dates occurred.

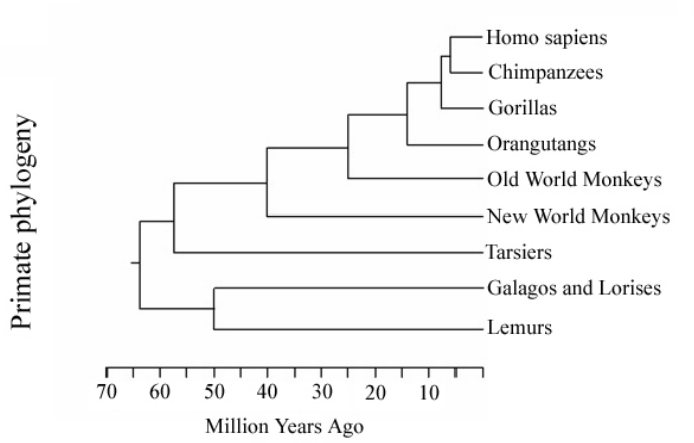

Figure 1. Primate phylogeny with divergence dates expressed in million years ago. The lemurs' closest relatives are galagos and lorises (adapted from Horvath & Willard, 2007).

6.1.2 Evolution and distribution

Lemurs are endemic to Madagascar and are not found in the wild anywhere else in the world (Yoder, 2007). Madagascar is the fourth largest island in the world (Horvath & Huntington, 2007) and ringtailed lemurs occur mostly in the southern third of the island (Jolly et al., 2006)

All the members of the family *Lemuridae* seem to origin from a common ancestor that arrived to Madagascar in the Cenozoic era over 60 million years ago (Yoder, 2007). At this time, Madagascar was already separated from other landmasses and the lemurs are believed to have dispersed to the island through rafting (Yoder, 2007). According to the same author there is, to date, still uncertainty about how many species of lemurs there are; in 1994 there were 33 identified lemur species, but twelve years later, in 2006, 70 living species had been identified (Yoder, 2007). When biologists can overcome the challenging task of recognizing and defining species even further division of lemur species may be expected (Yoder, 2007). Within the infraorder *Lemuriformes* there is a wide variety of physiological, morphological, ecological and behavioural features (Yoder, 2007). For example the smallest lemur, the mouse lemur, only weighs 50-60 grams and is an insectivore whereas the largest lemur, the indri, weighs up to 10 kg and is a browser (Yoder, 2007).

6.1.3. General description and morphometrics

According to Gould et al. (2003) wild ringtailed lemurs can reach an age of 18-20 years and females may live longer than males. There is only a slight sexual dimorphism between males and females (Sauther et al., 1999) due to the fact that females show external genitalia (Drea, 2007). However, all lemurs are sexually monomorphic regarding body mass (Kappeler, 1990) and both sexes reach similar sizes when adult (Drea, 2007). Dutton et al. (2003) showed that individuals within one population of wild ringtailed lemurs weighed about 1.15-2.45 kg and Wallach & Boever (1983) state that ringtailed lemurs can weigh from 800 g (infants) to 5.2 kg (adults). Their head and body length vary from 385-455 mm and their tail length can vary from 560-624 mm (Goodman, 2006). The front teeth in the lower jar have a formation of a tooth comb which is used by the animal while stripping vegetation and grooming (Cuozzo & Sauther, 2006).

The ringtailed lemur has unique features among the *Lemuridae* such as a long, black and white ringed tail and a long facial skeleton (Eaglen & Groves, 1988). The colours of the ringtailed lemurs' back vary from grey to a light red-brown (Mittermeier et al., 2008). They have a white underside, the neck and the crown are dark grey and the haunches and limbs are grey (Mittermeier et al., 2008). Figure 2. shows the unique features of the ringtailed lemur; the black and white ringed tail.

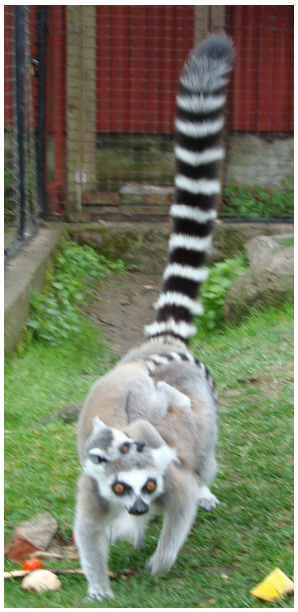

Figure 2. Ringtailed lemur mother with infant. Photo: Taina Thernström

6.1.4. Reproductive biology

Both females and males reach maturity at the same age, the first mating usually occurs at the age of 2.5-3 years and the mating system is promiscuous (Drea, 2007). The females gestate for about 135 days (Starling et al., 2010) during the dry season when the food availability is low (Cavigelli et al., 2003). They give birth during the transition from the dry to the wet season (Cavigelli et al., 2003) when there is plenty of food (Sauther et al., 1999). Females lactate during the period of food abundance (Sauther et al., 1999) and when the infants are about 6 weeks of age they self-feed more independently and they can benefit both from the mother's milk and other food resources (Gould, 1990).

6.1.5. Habitat, threats and conservation

In the southern part of Madagascar the wet season lasts from November to March and the annual temperature averages 25°C (Sussman, 1991). The temperature varies though, with high temperatures (35°C) in the wet season and lower temperatures (between 3°C at night and 23°C) in the dry season (Sussman, 1991). Due to the different climate regimes with very hot and cold weather (Goodman et al., 2006) and fluctuations in rain and food availability (Pride, 2005), the ringtailed lemurs have adapted to different habitats (Goodman et al., 2006). As a result the ringtailed lemur is often found in habitats such as rock canyons, anthropogenic (man-made) savannas, deciduous (broad-leaved) forests, gallery (corridor) forests and spiny (thorn) bushes (Goodman et al., 2006). Rivers are not a limiting factor for the distribution of the lemurs and they even seem to use them as dispersal corridors (Goodman et al., 2006). The home ranges of wild ringtailed lemurs vary from 6 to 30 ha with seasonal expansions and the population densities vary from 90-350 individuals/km² depending on the surroundings and the resources (Sussman, 1991).

Lemurs are to some extent protected from hunting through a cultural malagasy taboo, a fady (Hawkins et al., 1990). Fady is an umbrella term for different prohibitions and fady is an important mean in the work for the conservation of malagasy species (Jones et al., 2008).

The ringtailed lemur is included in the CITES appendices and that means that they are protected by the regulations of international trade of live specimens, derivatives and parts. The ringtailed lemur is also listed as “Near threatened” on the IUCN red list. Over the last 24 years the species is supposed to have declined approximately 20-25 % and is still decreasing (IUCN). According to Jolly et al. (2006) there were above 930 000 ringtailed lemurs within an area of 100 000 km² in Madagascar in 1985 whereas, the number had dropped to just above 750 000 fifteen years later, in 2000.

6.2. Behaviour

6.2.1. Foraging

Due to the different climate regimes on the island the ringtailed lemur is adapted to a varied diet (Goodman et al., 2006) and has been described as both an opportunistic omnivore (Sauther et al.,1992;1999) and frugivore/folivore (Simmen et al., 2006). According to Sauther et al. (1999) the ringtailed lemur feeds for example on leaves, fruits, flowers, spiders, birds and caterpillars. The feed consist of approximately 30-60% fruit, 30-51% herbs and leaves, 5-12 % flowers and less than 3% insects (Sauther et al., 1999). Figure 3. shows a ringtailed lemur feeding on a pineapple.

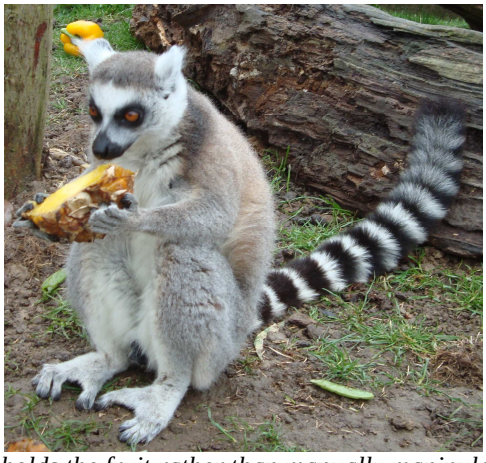

Figure 3. Notice how it simply holds the fruit rather than manually manipulate it. Photo: Taina Thernström

Ringtailed lemurs can be described as “semi-terrestrial”; they do most of the travel on the ground (Sauther, 1989), they are not as arboreal as other lemurs and they spend 18-30% of the time foraging on the ground (Sauther et al., 1999). A study by Pinkus et al. (2006) showed that when a population of ringtailed lemur at the Berenty reserve on Madagascar foraged up in the trees they mostly did it at a height of 10-15 m.

Since the island can not provide a regular supply of fresh water the ringtailed lemur can utilize water found in tree hollows (Sauther et al., 1999) from night dew and even from consumed foods (Goodman et al., 2006). When it comes to drinking from tree hollows the ringtailed lemurs immerse their hands or tail into the hole, withdraw them and then lick the water from them (Sauther et al., 1999).

6.2.2. Social structure

The lemur species that are both diurnal and tend to move in open areas usually have large social groupings (Martin, 1972) and among the strepsirrhine primates the ringtailed lemurs have the most complex social organization (Scordato & Drea, 2007). Ringtailed lemurs live together in multifemale and multimale social structures where females regardless of rank are dominant over males (Drea, 2007) and males do not show parental care (Cavigelli & Pereira, 2000).

In the wild, groups usually consist of 10-20 group members (Sussman, 1991) which is considered the optimal group size for wild ringtailed lemurs (Pride, 2005). The same author investigated the relationship between group size and cortisol levels (levels of a stress hormone) in free-ranging ringtailed lemurs and he found that females in small groups (from 5 animals) and in large groups (26 animals) had higher cortisol levels than females in intermediate groups (from 9, 14 and 19 animals). The costs for individuals in large groups are competition over food and mates and the costs for those in small groups are fewer partners to help defend territory or food patches against rivals (Pride, 2005). Males only exhibited increased cortisol levels due to group size during the courtship season and when competing over mates (Pride, 2005). When food is abundant all individuals within a group feed at the same time but if the resources are scarce the group members queue up waiting for their turn according to dominance (Sauther et al., 1999). Figure 4. shows two individuals foraging on the same pineapple at the same time.

Figure 4. These two individuals share the same food. Photo: Taina Thernström

Males migrate to other groups when sexually mature at about 3-4 years of age and they keep changing groups every 3.5 years (Gould, 2006). The ultimate reasons for the male migration

are probably the increased possibility of reproduction and the reduction of inbreeding and the proximate causes are rank improvement and sexual attraction to unrelated females (Gould, 2006). Several factors determine how a male chooses a new group, for example proximity (they tend to choose adjacent groups), number of mates and number of natal individuals in the new group (Gould, 2006). Male ringtailed lemurs often disperse to a new group together with other males and thus avoid possible costs of dispersal such as starvation, predation and attacks from extragroup males (Gould, 2006).

Females stay within their original group when sexually mature (Sauther et al., 1999). Adult females, their offspring and sometimes sisters form small cliques (Cavigelli et al., 2003) that constitute the centre of the group (Sauther et al., 1999). There can be several such matrilines (a mother line) within a group and when groups become too large matrilines can evict each other which results in the groups splitting up (Sauther et al., 1999). A study by Ichino & Koyama (2006) showed that females were evicted from a group when there where 16 or more group members and a total of seven or more females.

When ringtailed lemurs sleep and rest they usually do it in pairs, family groups or multifemale-multimale groups (Scheumann et al., 2007). Animals high in the sleeping hierarchy receive more grooming and touching whereas animals low in the sleeping hierarchy initiate more touching (Hosey & Thompson, 1985).

A study by Rasamimanana et al. (2006) showed that ringtailed lemurs spend almost 50% of their time resting, approximately 25 % of their time foraging, almost 20% moving and travelling, approximately 5% sunbathing, 2% sleeping and 2% grooming. Sunbathing is often seen in mornings and throughout the day and is thought to decrease the prevalence of ectoparasites by raising the temperature to uncomfortable levels for the ectoparasites (Loudon et al., 2006). The reason for the high proportion of resting time could be due to energy conservation since ringtailed lemurs have a low basal metabolic rate (Rasamimanana, 2006).

6.2.3. Aggression

Aggression is an important element in the social behaviour of all primates and it can occur in a variety of contexts, for example intragroup (dominance interactions over mates and food resources), anti-predator behaviour, intergroup resource defence and it can also be self-directed such as self-mutilation (Honess & Marin, 2006a).

Due to the promiscuous reproductive system males are forced to participate in agonistic and chaotic competitions with each other when competing over females and this results in regular changes in dominance rank and social challenges (Cavigelli & Pereira, 2000).

According to Jolly (1998) ringtailed lemurs seem to have just a couple of “close friends” and the relationships between two lemurs are either affiliative or agonistic. When females are pregnant the aggression levels are at their lowest but when the birth season come and the nutritional needs are high the distinction between “friends and foes” sharpens (Jolly, 1998). Females are considered to take the most active role in conflicts both between and within troops (Jolly, 1998) and when one matriline evicts other females from the group, the eviction is a result of a chain of aggressive episodes. Targeting aggression is a unique behaviour in lemurs of both sexes where an individual frequently attacks a specific member of the same sex which can result in injuries, eviction from the group or even death of the targeted individual (Jolly, 1998).

6.2.4. Communication and anti-predator behaviour

Ringtailed lemurs communicate via visualization, vocalization and olfactory signals (Sauther et al., 1999). Ringtailed lemurs (both infants and adults) show a wide array of different vocalization sounds and their vocal repertoire contains 28 different calls (Macedonia, 1993) e.g. chirps, shrieks, plosive barks, purrs, howls, squeals, me-ows, twitters, clicks (both with mouth closed and open) and rasps (Pereira & Macedonia, 1991). They have affiliative vocalizations, agonistic vocalizations and alerting and anti-predator vocalizations (Macedonia, 1993). Figure 5. shows a vocalizing ringtailed lemur.

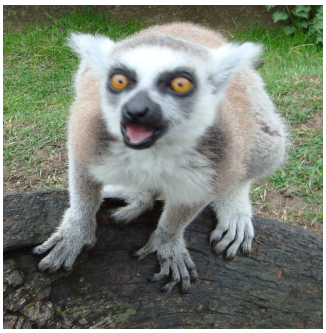

Figure 5. This ringtailed lemur is vocalizing with its mouth open. Photo: Taina Thernström

Ringtailed lemurs also communicate via olfactory signals from their specialized scent glands and they show complex scent-marking repertoires (Scordato & Drea, 2006). Saliva, faeces, urine and glandular secretions can give information about the signal senders sex, reproductive state, family membership, individual identity or territorial ownership (Scordato & Drea, 2006). According to Sauther et al. (1999) the primary motivation behind male signalling is supposed to be due to intrasexual competition whereas female signalling is supposed to show reproductive state. Male ringtailed lemurs have three scent glands (scrotal, brachial (arm) and antebrachial (lower arm)) where each type is thought to convey different information and females have a glandular field around their labia majora (Scordato & Drea, 2006). Males use the brachial and antebrachial glands to scent their tails so that they can wave them at each other during “male stink fights” (Sauther et al., 1999). Additionally, males have a spur next to the glands on their wrist and with the help of the glands and spur they scratch surfaces on trees leaving both visual and olfactory marks (Sauther et al., 1999).

A study by Pereira & Macedonia (1991) investigated the referential signalling hypothesis (that some prey species use different vocalizations when different predators are threatening them) on ringtailed lemurs. They found that lemurs use special calls in response to special categories of predators. For most primates are predation by carnivores, snakes and raptors a constant risk and the ringtailed lemur has native predators such as the fossa (Cryptoprocta ferox), the Madagascar boa constrictor (Boa manditra), the Madagascar harrier hawk (Polyboroides radiatus), the Madagascar buzzard (Buteo brachypterus) and the Madagascar serpent eagle (Eutriorchis astur) (Karpanty & Wright, 2007). Since the ringtailed lemur lives both on the ground and in trees, they are exposed to terrestrial, arboreal and avian predators (Sauther et al., 1999) and Pereira & Macedonia (1991) found that a terrestrial predator made them silently flee up in to a tree whereas an avian predator made them crouch to the ground and shriek.

6.2.5. Cognition

Cognition refers to the functions of learning, thinking and processing information in the brain.

Although some different types of research have been done on lemurs little is known about their cognition (Santos et al., 2005).

Santos et al. (2005) looked at ringtailed lemurs' ability of numerical understanding. The authors did a "1+1 addition event" which means that the subjects watched how two objects were placed behind an occluder. When the occluder was removed it either revealed both or only one object and the authors then measured how long the subjects looked at the items with the prediction that they would look longer at an impossible outcome. The results showed that ringtailed lemurs did look longer at impossible outcomes indicating that they have a capacity to understand simple mathematic functions (Santos et al., 2005).

Compared to apes the ringtailed lemurs show restricted adroitness in using the hands when handling food and they simply grasp and hold the food rather than manually manipulate it (Sauther et al., 1999). The results from a study by Fornasieri et al. (1990) showed that lemurs can learn to open uncomplicated bolts and to uncover food in a simple food-acquisition task. The authors found that the lemurs manipulated the boxes by scraping and scratching the lid open and they did not open boxes without food in them. The lemurs did not seem to learn from their trial-and-errors and used the same manoeuvres on the same location of the box which proves that the lemurs had a restricted understanding of the problem and the solution (Fornasieri et al., 1990).

A study by Merritt et al. (2007) showed that ringtailed lemurs have the memory mechanism of serial organization of information which means that they are able to remember the order of different events. The experiment was conducted on two female ringtailed lemurs that were exposed to a list of three, four or five photographs respectively (Merritt et al., 2007). Then the authors tested if the subjects selected the items in the correct order and the results showed that the two lemurs became better at learning the lists over time (Merritt et al., 2007).

Lemurs have a distinct natural and evolutionary history and there are many behavioural differences between lemurs and other primates. For example, lemurs have a high social intelligence and a variety of social behaviours but lack abilities to solve complicated tasks and puzzles (Dishman et al., 2009).

6.3. General husbandry in zoos

6.3.1. Status in the zoos and the species coordinator

Of all members of the family *Lemuridae* the ringtailed lemur is most abundant in zoos (Dishman et al., 2009) and this could be due to that they reproduce well and are considered easily manageable. The international species information system, ISIS, state that there were, on the 8th of April 2010, 2654 ringtailed lemurs in captivity in more than 300 zoos all over the world. According to the American association of zoos and aquaria (AZA), Catherina Spiezio, Bussolengo, Italy, has been the European species coordinator of ringtailed lemurs since 1994. Lynne Villers, Indianapolis Zoo, US, is the American species coordinator and she is also the studbook keeper (M. Mogilewsky, personal communication, 22 April 2010).

6.3.2. Environment and diet

According to Wallach and Boever (1983) the environmental temperatures in lemur holding facilities should be set at 18-26°C and Honess and Marin (2006a) advocate for temperature fluctuations during both day and night to promote natural behaviours such as resting during

hot days and crowding together during chilly nights. Most zoos in Sweden keep the temperatures at 20°C depending on whether it is summer or winter. The humidity requirements should preferably range from 55-70% (Wallach and Boever, 1983). Most primates originate from tropical regions and to imitate the day length the light should be provided on a 12:12 h light:dark cycle with phased transitions to imitate dawn and dusk (Honess & Marin, 2006a). An appropriate diet for lemurs in captivity is a commercial primate diet with the addition of vegetables and fruits (Wallach & Boever, 1983) and this is what most zoos in Sweden feed their ringtailed lemurs with.

6.3.3. Stress, stereotypic behaviour and animal-visitor interactions

According to Honess and Marin (2006) the biological responses with which an animal reacts to stressors can be concentrated through four channels: immunological, neuroendocrine, autonomic and behavioural and different individuals can respond in different ways to the same stimulus. Measurements of stress in animals have traditionally been quantified through cortisol levels in saliva, plasma, urine or faeces or by monitoring changes in blood pressure or heart rate (Honess & Marin, 2006).

There are many factors responsible for producing stress responses in animals in zoos, for example an unstimulating environment, predation threat, solitary housing, group composition changes and collection of blood samples (Honess & Marin, 2006). Stress has been shown to cause changes in animals' brain structures and function and immune competence (Honess & Marin, 2006).

Previous studies have shown that low-ranking male mammals experience more stress than high-ranking males (Cavigelli et al., 2003). However, more recent studies on group-living and free-ranging female mammals have shown that high-ranking females experience more stress than low-ranking females (Cavigelli et al., 2003). Possible explanations for this are that high ranking females are sole breeders that to go through energy-expensive processes such as ovulation, gestation and lactation and also that high ranking females have high aggressive levels which in turn increases corticoid levels (Cavigelli et al., 2003).

Captive animals that are unable to perform behaviours for which they are highly motivated to can develop abnormal behaviours compared to the behavioural repertoire of wild conspecifics. Such abnormal behaviours are called stereotypic behaviour and it has been described as "unvarying, repetitive behaviour patterns that have no obvious goal or function" and has been suggested as a way of adapting to and coping with an abnormal environment (Tarou et al., 2005). It can be divided into three categories: locomotor behaviour (for example pacing), appetitive behaviour (for example crib-biting) and self-injurious behaviour (for example self-mutilation) (Tarou et al., 2005). Causes of stereotypic locomotor behaviour are for example not being able to forage, search for mates, escape from other group members, lack of space or enrichments and many stereotypic behaviours are related to feeding routines (Tarou et al., 2005). The same authors investigated the stereotypic behaviour of 440 prosimians (representing 6 genera of lemurs including ringtailed lemur) in 48 institutions in USA and the results showed that 13.2 % displayed some stereotypic behaviour. Pacing was shown by 67.2%, somersaulting by 11.5% and overgrooming, self-injurious behaviour and "other" was shown by 18%.

Fernandez et al. (2009) noted that ring-tailed lemurs changed their behaviour whether visitors were absent or present and many captive primates respond negatively to noisy and large crowds (Tarou et al., 2009). The ringtailed lemurs displayed significant decreases in grooming

and affiliate behaviour and increases in activity and aggression when visitors where present (Tarou et al., 2009).

6.3.4. Swedish welfare regulations

There are several regulations concerning zoos when they keep animals for public exhibition. One of these regulations are; Regulations from the Swedish Board of Agriculture concerning keeping animals at zoo; Dnr L108

"Chapter 5. Primates
1 § There must be an off exhibit.
2 § Unless otherwise specified, at least half of the surface should be composed of soft soil or be soft. This applies to both indoor and outdoor enclosures.
3 § The outdoor enclosure should be equipped with protection from rain, wind and sun.
4 § The sizes of the nesting boxes should be large enough so that the primates can be stretched out to full length.
5 § All species can be kept in the indoor enclosures during low season."

"Chapter 5. Ringtailed lemurs
8 § Space requirements:

Indoor enclosure:	Volume 100 m^3; with a minimum surface area of 30 m^2 and a minimum height of 3 m.
Outdoor enclosure:	50 m^2, height 3 m.
Enclosure design:	Plenty of climbing and jumping possibilities, vertical and horizontal trunks and elevated nesting boxes."

Figure 6. shows an elevated nesting box.

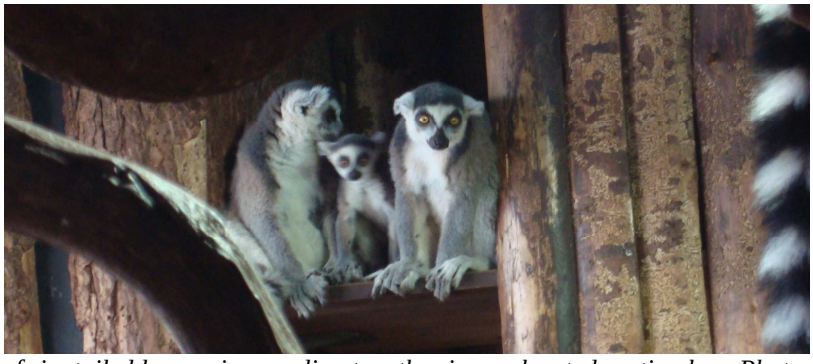

Figure 6. A group of ringtailed lemurs is crowding together in an elevated nesting box. Photo: Taina Thernström
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7. DISCUSSION

Since the ringtailed lemur is a threatened species it is possible that they are facing an extinction in the future (Jolly, 2006). Over 300 hundred zoos are currently housing ringtailed lemurs and these zoos play important roles; they function as gene banks, they educate visitors of the lemur situation and they conduct research on improving the welfare of captive lemurs. This literature study addresses zoos and how they can house ringtailed lemurs from the animals' point of views.

7.1. Enclosure design

When designing enclosures for lemurs there are many factors to consider for example what type of fence or barriers should be used, what size it should have, the location of the enclosure and what kind of furnishings there should be in it.

It is widely recognized that water moats prevent primates from escaping and hence zoos have been using moats as barriers for a long time (Hancocks, 1996). However, ringtailed lemurs are known to use rivers on Madagascar as dispersal corridors (Goodman, 2006) and consequently I do not recommend designing lemur enclosures with water moats as barriers. The most common way to keep ringtailed lemurs is to keep them in a fenced enclosure where the lemurs can use the fence as climbing possibilities whereas other zoos let their ringtailed lemurs range free in the zoo. Several factors such as potential predators (canines, felines, raptors) and animal-visitor interactions decide whether these approaches are appropriate or not.

Wild ringtailed lemurs have home ranges that vary from 6-30 ha (Sussman, 1991) and they do most of the travelling on the ground (Sauther, 1989). The Swedish animals welfare regulations state that the minimum surface area of the indoor enclosure should be at least 30 m^2, which is equivalent to 0,05% of the lemurs smallest natural home ranges. The Swedish welfare regulations also state that the minimum height is set at 3 m but studies have shown that wild ringtailed lemurs forage at a height of 10-15 m in trees (Pinkus et al., 2006). I suggest designing enclosures more equivalent to the lemurs' natural home ranges to promote the above-mentioned natural behaviours. I believe this would not only benefit the animals but also the zoos. According to Hosey (2005) visitors consider large enclosures as a positive feature since restricted space and the confinement and inability to roam freely is a negative perceived feature in the zoo environment.

Although most zoos in Sweden house ringtailed lemurs in both indoor and outdoor enclosures, according to the current animal welfare regulations zoos do not have to provide ringtailed lemurs with the possibilities to be outside during the low season. Keeping ringtailed lemurs inside during the low season prevent them from performing behaviours such as sunbathing when the sun is shining. The research material about sunbathing is scarce and we do not know how important this behaviour is and how motivated ringtailed lemurs are to perform it. However, we do know that wild ringtailed lemurs spend approximately 5% (1,2 h) of the day sunbathing (Rasamimanana et al., 2006) and I recommend providing ringtailed lemurs with possibilities to sunbath when the weather allows it until we know how important this behaviour is for them.

Wild ringtailed lemurs spend a large part of the day on the ground (Sauther, 1989;1999) and thus it is important to provide captive lemurs with possibilities to move around freely on the ground but also have access to nearby trees or other climbing opportunities if they become frightened. Examples of enclosure furnishings are perches, swings, platforms (Honess & Marin, 2006b) hammocks, ropes and trees. I suggest that the different furnishings are both stable and "moving" and of different shapes to mimic natural settings. I also recommend that zoos place barriers inside the enclosure to provide hiding places for animals e.g. when aggressive encounters take place. Examples of barriers are panels, walls with large holes in them, hanging sections of adequately materials, horizontal cylinders or elevated platforms big enough for only one individual.

Wild ringtailed lemurs can spend up to 50% of their time resting (Rasamimanana et al., 2006) and thus it is important to provide them with nesting boxes where they feel both safe and comfortable. I suggest providing groups of lemurs with multiple nesting boxes in different shapes, with different substrates and placed at different heights above the ground to investigate which nesting box they find most suitable. The substrate should be warm and dry and the nesting boxes should be big enough for all the group members to huddle together. I suggest that the nesting boxes are positioned high up from the ground and that the opening is almost directed away from the visitors because the lack of possibilities to move away from human visitors are known to cause stress in captive animals (Morgan & Tromborg, 2007).

In the same way, I suggest that the exhibit enclosure has three sides away from public view so that the animals have enough space to retreat within their flight distances. I also suggest that there should be plenty of elevated surfaces so that the animals can look down on visitors and not the other way around. By making sure that the captive animals have sufficient retreat space and subsequently feel that they both have control over and can cope with the situation the zoos can improve the animal welfare (Morgan & Tromborg, 2007). I also recommend limiting the number of visitors in front of the enclosures and inform the visitors about how to behave and not which can reduce stress for the animals.

Ethological observations of animal-visitor interactions are important. One could expect that stress would be displayed by behaviours such as throwing objects at visitors or performing obvious lunges at the visitors but stress may instead be displayed through increased walking and decreased grooming and foraging when visitors are present, which could be hard to detect without doing proper behavioural studies.

I propose that several changes should be made regarding the Swedish welfare regulations concerning animals kept at zoos; the minimum measurements of the enclosures should be increased, the lemurs should have access to outdoor enclosures all year round and they must have access to hiding places and several nesting boxes.

7.2. Environmental enrichment

Besides designing an appropriate enclosure for the lemurs, it is important to provide them with something to do in it. Environmental enrichment can be defined as "a practice aiming to provide environments of greater physical, temporal and social complexity that affords animals more of the behavioural opportunities found in the wild" (Honess & Marin, 2006b).

Both Cavigelli et al. (2003) and Sauther et al. (1999) describe the ringtailed lemur as diurnal whereas Horvath and Huntington (2007) describe it as cathemeral (e.g. both day and night active). Depending on whether the animal is a diurnal or a cathemeral species their cognitive abilities vary (MacLean et al., 2009). According to the same authors, by being cathemeral, the species must have flexible behavioural strategies to be able to solve more problems than a diurnal species. MacLean et al. (2009) state that intelligent behaviour rather than instincts is if a species can adapt to a changing environment on demand. Although the scientists have different opinions of the activity pattern of the ringtailed lemur, the environment of captive lemurs should be complex and enriched.

One way of enriching the environment for captive lemurs is the use of feeding enrichment. There is not much research done on feeding enrichments in lemurs (Dishman et al., 2009; Fornasieri, 1990). Because of this, several of the following examples of feeding enrichments mentioned below are adapted from other primates. One variation of feeding enrichment is to provide novel foods in novel ways. Examples of feeding enrichments for other primates are: unhusked corn, peanuts in shell, frozen fruit ("ice cream" for animals), Kong toys (dog toys made of rubber) filled with frozen juice (Honess & Marin, 2006b) and juice or peanut butter daubed high up on the trees. I suggest using these feeding enrichments for ringtailed lemurs as well. Another appreciated enrichment for many other primates is paper-wrapped cardboard boxes filled with straw and a couple of grapes in them. The animals have to open the "present" and search for the grapes within it. A shallow tank could function as an environmental enrichment; a curious individual could try to retrieve floating food or "fish" for it on the bottom. There are a variety of different dog toys on the market that could be used for lemurs and I suggest using those that are time and energy consuming for the animals but not too complicated. I suggest that the enrichments provided outnumber the number of individuals to avoid aggressive competition.

Feeding enrichments that has shown to decrease aggression and stereotypic behaviour and at the same time increase the foraging time in other primates are food (e.g. grain, sunflower seeds, meal worms) mixed into a forage substrate or scattered food on the top of the mesh roof and in trees or bushes (Honess & Marin, 2006b). A study by Dishman et al. (2009) found that adding browse in an enclosure of ringtailed lemurs promoted more activity and foraging and consequently I propose adding browse in the enclosures.

Since lemurs have evolved to spend almost 30% (8 hours) of the day foraging (Rasamimanana et al., 2006) I suggest feeding them morning, afternoon and evening so that the number of feedings are spread out throughout the day (e.g. ad lib pellets, vegetables and fruits). Between the feedings different foods or foraging tasks that are time and energy consuming should be provided so that the lemurs have the possibilities to perform foraging behaviours throughout much of the day.

I believe that another way of enriching the environment and improve the welfare of captive ringtailed lemurs is to train them. Most if not all of the ringtailed lemurs kept in Swedish zoos today have been born in captivity and these individuals are not likely to be let out in to the wild. Instead of the animal keepers and the lemurs experience handling, daily health checks or veterinary examinations as stressful, these procedures should be facilitated by regular clicker training and positive reinforcement. The zoologist or the animal keepers of the zoo should be educated in how to train animals with the help of clicker training and positive reinforcement. The use of clicker training may decrease the stress of the lemurs while handling them and instead introduce a new type of positive experience and enrichment into the daily life of

captive lemurs. Clicker training can make the animals feel more in control of the situation, resulting in a reduction of its stress levels (Prescott et al., 2005). Clicker training (a trainer "catches" a wanted behaviour with a clicker), targeting (an animal is trained to touch a special target for example a mark or a stick) and shaping (letting an animal figure out what the trainer wants it to do rather than showing the animal what to do) are well known enrichment methods for numerous animals including primates (Prescott et al., 2005).

In husbandry manuals, focus often lies on husbandry such as handling and health, housing and dietary requirements of the animals but surprisingly little is written about their behaviour. I propose that behaviour and examples of enrichments will constitute larger parts of the husbandry manuals in the future and I also suggest that other chapters will take ethology in consideration to a larger extent than they do today.

7.3. Optimal social structures

Since the ringtailed lemur is a group-living species and has a high social intelligence, social interactions are not just key elements in their behavioural repertoire but also one of the best types of enrichment in a stabile group. Grooming, upbringing of infants and play fighting are examples of energy-consuming social behaviours that require the use of different cognitive abilities.

The optimal group size in the wild is 10-20 group members (Pride, 2005) and this is valid when the ringtailed lemurs' territories range from 6-30 ha (Sussman, 1991). However, zoos have difficulties providing large enclosures similar in size to the wild territories and consequently they can not house groups consisting of this many individuals. Competition for food resources is also a factor determining group size (Pride, 2005) and thus it is important for the zoo to make sure that there is both plenty of food and that it is distributed or scattered over a large area so that all individuals can eat at the same time. When groups become too large (more than 16 members or 7 or more adult females) matrilines can evict each other through frequent aggressive encounters (Ichino & Koyama, 2006). I suggest keeping groups with 10-15 members and with no more than 7 adult females to avoid that aggressive encounters result in attempted evictions.

Wild ringtailed lemurs live together in multifemale and multimale social structures and the mating is promiscuous (Drea, 2007) and thus it is important to try to keep track of which male is fathering which offspring to prevent inbreeding (e.g. father-daughter) in zoos. In the wild, males often disperse from their natal group when they reach maturity (Gould, 2006) and it is important for the species coordinator and the zoos to be aware that the males are probably highly motivated to do this. The males continue to migrate approximately every 3.5 years (Gould, 2006) and if they stay in their natal group aggressive encounters or targeting aggression are likely to occur around this time. Exchanges of males between zoos every third year could be a solution to both the inbreeding problem and the migration.

The Swedish welfare regulations concerning animals kept at zoos do not mention anything about lemur group size or enrichments although there are many institutions currently housing ringtailed lemurs in Sweden. Hence, Swedish zoos today differ in their ways of enriching the environment of the lemurs and setting a research-based basic standard could help the zoos to house healthy ringtailed lemurs.

Even if this study is a literature study and has the disadvantage of not contributing to the already existing research, I have found that there is a lack of research in areas such as sunbathing and nesting behaviour. To my knowledge, no research about nesting behaviour in ringtailed lemurs have been conducted and we do not know if females want to give birth in the presence of the group or by her self. For the females' and the infants' welfare, I suggest providing the enclosure with extra nesting boxes until the ecology of the nesting behaviour has been fully mapped.

Ringtailed lemurs are unusual as laboratory animals compared to other primates, probably because the social ringtailed lemurs do not manage very well when being housed singly in barren enclosures and the results would probably be biased. If more research on wild ringtailed lemur behaviour were done it could improve the welfare and well-being of captive ringtailed lemurs.

Many articles about lemurs are published in magazines such as "Human evolution" and it seems that primate studies are often a tool of understanding the human evolution and not studies of the animals per se. This could explain why "unimportant" areas have been overlooked but nevertheless is the conducted research valuable to ethologists. One of the best ways to contribute to previous findings is to conduct ethological studies and by this way map the behavioural ecology of ringtailed lemurs and subsequently improve their welfare and well-being in captivity.

8. CONCLUSIONS

The conclusion of this literature study is that housing of ringtailed lemurs can be optimized from an ethological perspective when taking, enclosure design, environmental enrichments and social structures in consideration. An optimal group size should have between 10-15 group members with no more than 7 adult females. This group size requires large enclosures and food that is available for all members simultaneously as well as barriers for animals to hide behind when aggressive encounters takes place. The enclosures should have three sides away from public view, multiple nesting boxes and the lemurs should have access to the outdoor enclosure all year round. Besides providing the ringtailed lemurs with jumping and climbing possibilities there should be plenty of environmental enrichments in the enclosures. Examples of enrichments that could be used for lemurs are browse, many different dog toys and to present novel foods in novel ways. Clicker training could function both as enrichment and as a training method to help facilitate handling or veterinary examinations.

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10. REFERENCES

Cavigelli, S., A., Dubovick, T., Levash, W., Jolly, A. & Pitts, A. 2003. Female dominance status and fecal corticoids in a cooperative breeder with low reproductive skew: ring-tailed lemurs (Lemur catta). Hormones and Behavior. 43, 166-179.

Cavigelli, S., A. & Pereira, M., E. 2000. Mating season aggression and fecal testosterone levels in male ring-tailed lemurs (Lemur catta). Hormones and Behavior. 37, 246-255.

Cuozzo, F., P. & Sauther, M., L. 2006. Severe wear and tooth loss in wild ring-tailed lemurs (Lemur catta): A function of feeding ecology, dental structure and individual life history. Journal of Human Evolution. 51, 490-505.

Dishman, D., L., Thomson, D., M. & Karnovsky, N., J. 2009. Does simple feeding enrichment raise activity levels of captive ring-tailed lemurs (Lemur catta)?. Applied Animal Behaviour Science. 116, 88-95.

Drea, C., M. 2007. Sex and seasonal differences in aggression and steroid secretion in Lemur catta: Are socially dominant females hormonally “masculinized”?. Hormones and behavior. 51, 555-567.

Dutton, C., J., Junge, R., E. & Louis, E., E. 2003. Biomedical evaluation of free-ranging ring-tailed lemurs (Lemur catta) in Tsimanampetsotsa strict nature reserve, Madagascar. Journal of Zoo and Wildlife Medicine. 34, 16-24.

Eaglen, R., H. & Groves, C., P. 1988. Systematics of the Lemuridae (Primates, Strepsirhini). Journal of Human Evolution. 17, 513-538.

Fernandez, E., J., Tamborski, M., A., Pickens, S., R. & Timberlake, W. 2009. Animal-visitor interactions in the modern zoo: Conflicts and interventions. Applied Animal Behaviour Science. 120, 1-8.

Fornasieri, I., Anderson, J., R. & Roeder, J., J. 1990. Responses to a novel food acquisition task in three species of lemurs. Behavioural Processes. 21, 143-156.

Garcia, G. & Goodman, S., M. 2003. Hunting of protected animals in the Parc National d’Ankarafatsika, north-western Madagascar. Oryx. 37, 115-118.

Goodman, S., M., Rakotoarisoa, S., V. & Wilmé, L. 2006. The distribution and biogeography of the ringtailed lemur (Lemur catta) in Madagascar. In: Ringtailed lemur biology: Lemur catta in Madagascar. (Eds. Jolly, A., Sussman, R., W., Koyama, N. & Rasamimanana, H.). Springer. Chicago.

Gould, L. 1990. The social development of free-ranging infant Lemur catta at the Berenty reserve, Madagascar. International Journal of Primatology. 11, 297-318.

Gould, L., Sussman, R., W. & Sauther, M., L. 2003. Demographic and Life-History Patterns in a Population of Ring-Tailed Lemurs (Lemur catta) at Beza Mahafaly Reserve, Madagascar: A 15-Year Perspective. American Journal of Physical Anthropology. 120, 182-194.

Gould, L. 2006. Male sociality and integration during the dispersal process in Lemur catta: A case study. In: Ringtailed lemur biology: Lemur catta in Madagascar. (Eds. Jolly, A., Sussman, R., W., Koyama, N. & Rasamimanana, H.). Springer. Chicago.

Hancocks, D. 1996. The design and use of moats and barriers. In: Wild mammals in captivity: Principles and techniques. (Eds. Kleiman, D., G., Allen, M., E., Thompson, K., V., Lumpkin, S & Harris, H.). The university of Chicago press. Chicago.

Hawkins, A., F., A., Chapman, P. & Ganzhorn, J., U. 1990. Vertebrate conservation in Ankarana special reserve, northern Madagascar. Biological Conservation. 54, 83-110.

Honess, P., E. & Marin, C., M. 2006. Behavioural and physiological aspects of stress and aggression in nonhuman primates. Neuroscience and Biobehavioral Reviews. 30, 390-412.

Honess, P., E. & Marin, C., M. 2006. Enrichment and aggression in primates. Neuroscience and Biobehavioral Reviews. 30, 413–436
Horvath, J., E. & Huntington, F., W. 2007. Primate comparative genomics: lemur biology and evolution. TRENDS in Genetics. 23, 173-182.
Hosey, G., R. & Thompson, R., J. 1985. Grooming and touching behaviour in captive ring-tailed lemurs (Lemur catta L.). Primates. 26, 95-98.
Hosey, G., R. 2005. How does the zoo environment affect the behaviour of captive primates? Applied Animal Behaviour Science. 90, 107-129
Hosey, G., Melfi, V. & Pankhurst, S. 2009. Zoo animals: Behaviour, management and welfare. Oxford university press. Oxford.
Ichino, S. & Koyana, N. 2006. Social changes in a wild population of ringtailed lemurs Lemur catta) at Berenty, Madagascar. In: Ringtailed lemur biology: Lemur catta in Madagascar. (Eds. Jolly, A., Sussman, R., W., Koyama, N. & Rasamimanana, H.). Springer. Chicago. ISBN 0387326693.
Jolly, A. 1998. Pair-bonding, female aggression and the evolution of lemur societies. Folia Primatologica. 69, 1-13.
Jones, J., P., G., Andriamarovololona, M., M. & Hockley, N. 2008. The importance of taboos and social norms to conservation in Madagascar. Conservation Biology. 22, 976-986.
Kappeler, P, M. 1990. The evolution of sexual size dimorphism in prosimian primates. American Journal of Primatology. 21, 210-214.
Kappeler, P., M. 1990. Short communications: Social status and scent-marking behaviour in Lemur catta. Animal Behaviour. 40, 774-776.
Karpanty, S., M. & Wright, P., C. 2007. Predation on Lemurs in the Rainforest of Madagascar by Multiple Predator Species: Observations and Experiments. In: Primate anti-predator strategies. (Eds. Gursky, S., L. & Nekaris, K., A., I.). Springer. Virginia.
Loudon, J., E., Sauther, M., L., Fish, K., D., Hunter-Ishikawa, M. & Ibrahim, Y., J. 2006. One reserve, three primates: applying a holistic approach to understand the interconnections among ring-tailed lemurs (Lemur catta), Verreaux's sifaka (Propithecus verreauxi), and humans (Homo sapiens) at Beza Mahafaly Special Reserve, Madagascar. Ecological and Environmental Anthropology. 2, 53-74.
Macedonia, J., M. 1993. The vocal repertoire of the ring-tailed lemur (Lemur catta). Folia Primatologica. 61, 186-217.
MacLean, E., V., Barrickman, N., L., Johnson, E., M. & Wall, C., E. 2009. Sociality, ecology and relative brain size in lemurs. Journal of Human Evolution. 56, 471-478.
Martin, R., D. 1972. Adaptive radiation and behaviour of the Malagasy lemurs. Philosophical Transactions of the Royal Society of London. Biological Sciences. 264, 295-352
Merritt, D., MacLean, E., L., Jaffe, S. & Brannon, E., M. 2007. A comparative analysis of serial ordering in ring-tailed lemurs (Lemur catta). Journal of Comparative Psychology. 121, 363-371.
Mittermeier, R., A., Ganzhorn, J., U., Konstant, W., R,. Glander, K., Tattersall, I., Groves, C., P., Rylands, A., B., Hapke, A, Ratsimbazafy, J., Mayor, M., I., Louis Jr, E., E., Rumpler, Y., Schwitzer, C. & Rasoloarison, R., M. 2008. Lemur diversity in Madagascar. International Journal of Primatology. 29, 1607-1656.
Morgan, K., N. &. Tromborg, C., T. 2007. Sources of stress in captivity. Applied Animal Behaviour Science. 102, 262–302.
Muldoon, K., M. 2010. Paleoenvironment of Ankilitelo Cave (late Holocene, south-western Madagascar): implications for the extinction of giant lemurs. Journal of Human Evolution. 58, 338-352.
Pereira, M., E. & Macedonia, J., M. 1991. Ringtailed lemur anti-predator calls denote predator class, not response urgency. Animal Behavior. 41, 543-544.

Pride, R., E. 2005. Optimal group size and seasonal stress in ring-tailed lemurs (Lemur catta). Behavioral Ecology. 550-560.
Pinkus, S., Smith, J., N., M. & Jolly, A. 2006. Feeding competition between introduced Eulemur fulvus and native Lemur catta during the birth season at Berenty reserve, southern Madagascar. In: Ringtailed lemur biology: Lemur catta in Madagascar. (Eds. Jolly, A., Sussman, R., W., Koyama, N. & Rasamimanana, H.). Springer. Chicago.
Prescott, M., J., Bowell, V., A. &Buchanan-Smith, H., M. 2005. Training laboratory-housed non-human primates, part 2: Resources for developing and implementing training programmes. Animal Technology and Welfare. 133-148.
Rasamimanana, H., Andrianome, V., N. Rambeloarivony, H & Pasquet, P. 2006. Male and Female Ringtailed Lemurs' Energetic Strategy Does Not Explain Female Dominance. In: Ringtailed lemur biology: Lemur catta in Madagascar. (Eds. Jolly, A., Sussman, R., W., Koyama, N. & Rasamimanana, H.). Springer. Chicago.
Sauther, M., L. 1989. Antipredator behavior in troops of free-ranging Lemur catta at Beza Mahafaly special reserve, Madagascar. International Journal of Primatology. 10, 595-606.
Sauther, M., L., Sussman, R., W. & Gould, L. 1999. The Socioecology of the Ringtailed Lemur: Thirty-five Years of Research. Evolutionary Anthropology. 120-132
Sauther, M., L. Fish, K., D., Cuozzo, F., P., Miller, D., S., Hunter-Ishikawa, M. & Culbertson, H. 2006. Patterns of health, disease and behavior among wild ringtailed lemurs, Lemur catta: Effects of habitat and sex. In: Ringtailed lemur biology: Lemur catta in Madagascar. (Eds. Jolly, A., Sussman, R., W., Koyama, N. & Rasamimanana, H.). Springer. Chicago.
Santos, L., R., Barnes, J., L. & Mahajan, N. 2005. Expectations about numerical events in four lemur species (Eulemur fulvus, Eulemur mongoz, Lemur catta and Varecia rubra). Animal Cognition. 8, 253-262.
Scheumann, M., Rabesandratana, A. & Zimmermann, E. 2007. Predation, communication and cognition in lemurs. In: Primate anti-predator strategies. (Eds. Gursky, S., L. & Nekaris, K., A., I.). Springer US.
Scordato, E., S. & Drea, C., M. 2007. Scents and sensibility: information content of olfactory signals in the ringtailed lemur, Lemur catta. Animal Behaviour. 73, 301-314.
Simmen, B., Sauther, M., L., Soma, T., Rasamimanana, H., Sussman, R., W., Jolly, A., Tarnaud, L. & Hladik, A. 2006. Plant species fed on by Lemur catta in gallery forests of the southern domain of Madagascar. In: Ringtailed lemur biology: Lemur catta in Madagascar. (Eds. Jolly, A., Sussman, R., W., Koyama, N. & Rasamimanana, H.). Springer. Chicago.
Starling, A., P., Charpentier, M., J., E., Fitzpatrick, C., Scordato, E., S. & Drea, C., M. 2010. Seasonality, sociality and reproduction: Long-term stressors of ring-tailed lemurs (Lemur catta). Hormones and Behavior. 57, 76-85.
Sussman, R., W. 1991. Demography and social organization of free-ranging Lemur catta in the Beza Mahafaly reserve, Madagascar. American Journal of Physical Anthropology. 84, 43-58.
Tarou, L., R., Bloomsmith, M., A. & Maple, T., L. 2005. Survey of stereotypic behavior in prosimians. American Journal of Primatology. 65, 181-196.
Wallach, J., D. & Boever, W., J. 1983. Diseases of exotic animals: Medical and surgical management. Saunders company. Philadelphia.
Yoder, A., D. 2007. Lemurs. Current Biology. 17, 866-868.

Internet sites
International Union for Conservation of Nature and Natural Resources, IUCN red list, http://www.iucnredlist.org/apps/redlist/details/11496/0, visited 2010-04-14.

International Species Information System, ISIS, http://app.isis.org/abstracts/abs.asp, visited 2010-04-20.

The Convention on International Trade in Endangered Species of Wild Fauna and Flora, CITES, http://www.cites.org/gallery/species/mammal/mammals.html, visited 2010-04-20.

Welfare regulations
Regulations from the Swedish Board of Agriculture concerning keeping animals at zoos (SJVFS 2009:92) Dnr L108.